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Estimation of Heritabilities, Genetic Correlations, and Response to Selection for Growth, Body Size, and Processing Traits in Red Swamp Crawfish, *Procambarus Clarkii* (Girard).

Charles Gregory Lutz

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Estimation of heritabilities, genetic correlations, and response to selection for growth, body size, and processing traits in red swamp crawfish, *Procambarus clarkii* (Girard)

Lutz, Charles Gregory, Ph.D.

The Louisiana State University and Agricultural and Mechanical Col., 1987

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ESTIMATION OF HERITABILITIES, GENETIC CORRELATIONS,
AND RESPONSE TO SELECTION FOR GROWTH,
BODY SIZE, AND PROCESSING TRAITS
IN RED SWAMP CRAWFISH,
PROCAMBARUS CLARKII (GIRARD)

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
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in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The School of Forestry, Wildlife, and Fisheries

by
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B.A., Earlham College, 1979
M.S., Louisiana State University, 1983
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ABSTRACT

Potential for genetic improvement of red swamp crawfish, Procambarus clarkii, and the possibility of negative selection for growth in cultured stocks as a result of harvesting practices have recently been the subject of speculation. This study provided indications of the potential for improvement of growth and processing traits in P. clarkii through selection.

After 150 days growout in fiberglass pools planted with rice (Oryza sativa), P. clarkii from each of 39 full-sib families nested within 15 half-sib families were weighed and measured for total length, carapace length, carapace width, abdomen width, abdomen depth, chela length, chela width, abdomen meat weight, and dressout percentage. Total length and weight were adjusted for density at harvest; other traits were adjusted for total length.

Heritabilities of traits were estimated from a nested analysis of variance for all animals combined and for reproductively mature (Form I) males, immature (Form II and juvenile) males, and females separately. Genetic and environmental correlations and heritabilities of traits were estimated for all animals combined using mixed model analysis with sex and male maturity as fixed effects.

Broodstock were selected from full-sib families for family selection and 5 replicates of mass selection for growth in length. Three replicates of mass selection and one replicate each of one-way positive and negative family selection produced sufficient offspring

to determine responses. Offspring were stocked for growout into replicate pools. Differences between lines in total length, weight and dressout percentage were analyzed within each replicate.

Sire heritability estimates for growth and body size traits for all animals combined were not significant ($P > 0.05$); estimates from mixed model analysis agreed with those from the nested analysis. Genetic correlations between growth in length and processing traits were positive and highly significant ($P < 0.01$). In spite of moderate to high selection intensities (0.74 to 4.57), no response for growth in total length was observed. Similarly, no trend of correlated response in dressout percentage could be discerned. Results suggest P. clarkii exhibits little additive variation in growth traits, although genetic gains in dressout percentage may be possible.

INTRODUCTION

Red swamp crawfish, Procambarus clarkii, is the only crustacean species supporting a profitable, large-scale aquaculture industry in North America. Red swamp crawfish is a large and aggressive species occurring naturally in a wide variety of habitats from northern Mexico to eastern Florida and northward to southern Illinois (Hobbs 1974)¹. When hydrological conditions are conducive to reproduction and survival, this species is harvested for food from natural habitats in Louisiana, especially the Atchafalaya basin.

P. clarkii has been widely introduced beyond its natural range within and outside of the U.S. (Huner and Barr 1984). Red swamp crawfish sustains a large semi-intensive fishery in rice producing areas of southern Spain, and introduced populations of this species have become well-established in Kenya, Hawaii and Japan. These populations are generally not utilized for food; rather, they are considered pests (Huner and Barr 1984). The degree to which other introduced populations of P. clarkii are utilized locally for food probably varies, although many entrepreneurs have expressed intentions of introducing this species into tropical areas to provide a crop specifically for export to the European market.

In recent years, agricultural production of Procambarid crawfishes (P. clarkii and, to a lesser extent, the white river

¹ Citation, Table, Figure and Bibliographic styles throughout follow those of Aquaculture.

crawfish, *P. acutus*) in rice fields, cane fields, or on marginal lands has expanded. This industry now occupies over 50,000 ha in the U.S., the majority of which are located in Louisiana and other states in the lower Mississippi valley. Pond production of crawfish in the U.S. approached 27 million kg during the 1985-1986 season (Louisiana Cooperative Extension Service 1986). Yields vary greatly among commercial ponds, but have been reported as high as 4000 kg/ha (Huner and Barr 1984).

As traditional agronomic crops have become less profitable and markets for crawfish have expanded, the incentive has increased to convert existing agricultural lands into crawfish production ponds. Growth of the crawfish industry in Louisiana during the past 2 decades has resulted in the creation of numerous jobs and a substantial economic boost to a sagging agricultural economy. Support industries such as harvesting supplies, processing, and marketing have become well-established in Louisiana.

As with other agricultural crops, investigation of genetic control over production characters and potential for genetic improvement of these characters in crawfish will be indispensable as the industry expands. Many researchers and producers believe current harvesting practices, resulting in the survival of slower growing animals to serve as broodstock for the following season, are imposing continuous negative selection for growth on cultured stocks. Speculation over the potential for increased yields through genetic improvement has been widespread in recent years. Improvement of agricultural species, both plant and animal, through genetic selection

is widely practiced. Accordingly, most producers and researchers in the agricultural sector, as well as the public in general, assume that any species which lends itself to culture may be improved upon through selective breeding. This may not be the case, however, for crawfish species in general. Various systematic and taxonomic studies including numerous species of Cambarid and Astacid crawfishes have consistently indicated that crawfish exhibit extremely low genetic variation as determined by average heterozygosity levels (Nemeth and Tracey 1979, Brown 1981, Attard and Pasteur 1984).

This study was conducted to evaluate genetic control over growth, body size, and processing traits in P. clarkii, and to determine the potential for genetic improvement in this species. Specific objectives were to:

1. estimate heritabilities for growth, body size, and processing traits in P. clarkii through sib analysis,
2. estimate genetic correlations for growth, body size, and processing traits in P. clarkii through sib analysis, and
3. measure selection response and realized heritability for growth in P. clarkii after one generation of replicated family and mass selection.

STUDY I:
ESTIMATION OF HERITABILITIES FOR GROWTH, BODY SIZE, AND PROCESSING
TRAITS IN RED SWAMP CRAWFISH, PROCAMBARUS CLARKII (GIRARD)

ABSTRACT

Lutz, C.G., and W.R. Wolters, 1987. Estimation of heritabilities for growth, body size, and processing traits in red swamp crawfish, Procambarus clarkii (Girard).

A random sample of 30 third instar red swamp crawfish, Procambarus clarkii, from each of 39 full-sib families nested within 15 half-sib families, was stocked into a separate 2.4-m diameter fiberglass pool planted with rice (Oryza sativa). Full-sib families were produced by randomly mating female crawfish to a pool of randomly chosen sires. Crawfish were harvested after 150 days and measured for total length, total weight, carapace width, carapace length, abdomen width, abdomen depth, chela width, chela length, abdomen meat weight, and dressout percentage. Total length and weight were adjusted for the effect of density within pools; other body size traits of individuals were adjusted for total length. Heritabilities were estimated for all animals combined and for reproductively mature (Form I) males, immature (Form II and juvenile) males, and females separately. Although non-additive sources of variation were found to influence all traits measured, all traits appear to show potential for at least moderate improvement through selection. Heritability

estimates suggest that important economic traits, growth in length and dressout percentage, might best be improved through some means other than mass selection.

INTRODUCTION

Since first attaining recognition as a legitimate agricultural endeavor in Louisiana in the early 1960's, crawfish culture has grown to occupy over 50,000 ha in the U.S. and pond production during the 1985-1986 season approached 27 million kg (Louisiana Cooperative Extension Service 1986). As optimal management techniques for pond production of crawfish become more widely practiced, several options will be available to further increase yields, including manipulation of seasonal reproductive cycles, more intensive management of forage and water quality, feeding formulated rations, and genetic improvement of cultured stocks.

No research has been published concerning the inheritance of quantitative traits such as growth rate and dressout percentage in crawfish. Black and Huner (1980) studied and described the qualitative inheritance of several color mutations in Procambarus clarkii and P. acutus acutus, all of which were transmitted as simple recessive alleles, and Craig (1985) examined sources of phenotypic variation in growth, body size, and processing traits in wild-caught families of P. clarkii.

Heritability estimates have several uses in animal husbandry, including the formulation of efficient breeding and stock management programs. In the crawfish industry, current problems such as stunted

populations could have a genetic basis. Objectives of this study were to estimate sire, dam, and broad sense heritabilities and their standard errors for growth, body size, and processing traits in P. clarkii. Results of this study should provide indications of the amount and type of genetic control over economically important traits and the types of breeding programs which will optimize genetic improvement of these traits in crawfish.

MATERIALS AND METHODS

During the spring and summer of 1985, 100 female P. clarkii were collected from ditches and experimental ponds at the Ben Hur Research Farm, Louisiana Agricultural Experiment Station, Baton Rouge, Louisiana. Females were held individually in 40-liter polyethylene tanks supplied with aerated pond water recirculated through a biological filter. Tanks were maintained at a temperature of 28-30 C, and animals were fed a commercial fish ration (32% protein) supplemented with carrots (Daucus carota) at 2 to 3 day intervals. Photoperiod was determined by natural sunrise and sunset with supplemental artificial lighting only during daylight hours; molting dates were recorded for each female.

Beginning on 1 September 1985, each of 18 males collected from ponds and ditches was mated to a separate group of 4 to 6 previously molted females. Upon molting, females lost any previously acquired spermatophores with their exuviae (Barnes 1974, Black and Huner 1979) allowing the production of full-sib families of known parentage. Matings were made in a random manner following techniques developed by

Black and Huner (1980) with one male introduced into a female's holding tank for approximately 48 hours and subsequently transferred to another female's holding tank. Eighty females were mated to 18 males within a 12-day period.

From 15 to 23 September 110 additional females with advanced cement gland development were collected from several ponds. Annuli ventrales were scrubbed with abrasive scouring pads and 95% ethanol to remove or destroy any previously acquired spermatophores (Berrill 1985); these females were then mated to 20 additional males collected from ditches. Each male was placed in a separate 160-liter tank with 6 females for a 5-day period, after which time females were isolated in partitioned 40-liter polyethylene tanks.

Mated females were initially maintained in lighted, uncovered tanks with circulating water in the presence of considerable day-to-day activity. On 11 October 1985, water circulation and aeration were discontinued, water level in holding tanks was reduced to 2.0 cm, and tanks were covered with black plastic to minimize disturbance and more closely approximate natural conditions in brood burrows. Females were checked for oviposition at 4-day intervals, and date of oviposition was recorded for all spawning females.

On 21 September 1985, 40 2.4-m diameter fiberglass pools were filled with river silt to a depth of 7 cm and planted with rice (Oryza sativa var. Leah) at a rate of 170 kg seed/ha to provide forage and cover for crawfish. Granulated 13-13-13 fertilizer was added in two applications to attain levels of 112 kg nitrogen per ha. On 27 November 1985, water levels in pools were increased to 40 cm, and

water hardness was adjusted to 150 mg/l as calcium carbonate with calcium chloride (de la Bretonne and Avault 1971).

Thirty, third-instar offspring were randomly selected from each of the 39 most contemporaneous full-sib families and stocked into a separate, randomly assigned pool to achieve a stocking rate of $6/m^2$, allowing comparisons with previous studies of P. clarkii in experimental pools (Clark et al. 1974, Craig 1985). Due to the need to maximize the number of full- and half-sib families in the analysis, full-sib families were not stocked into replicate pools. This confounding of common environment with dam effects was considered acceptable in light of the negligible effect of pool environment, exclusive of density, on traits to be measured in this study (Craig 1985).

Each pool was supplied with continuous diffused aeration at 0.15 m^3 per minute, and dissolved oxygen and temperature were checked weekly in all pools. Forage levels in individual pools were visually monitored, and 0.9 kg supplemental forage (mixed coarse hay) was added to each pool on 15 April to reduce the possibility of forage dissimilarity among pools and competition among full-sibs for limited resources within a common environment (Falconer 1981).

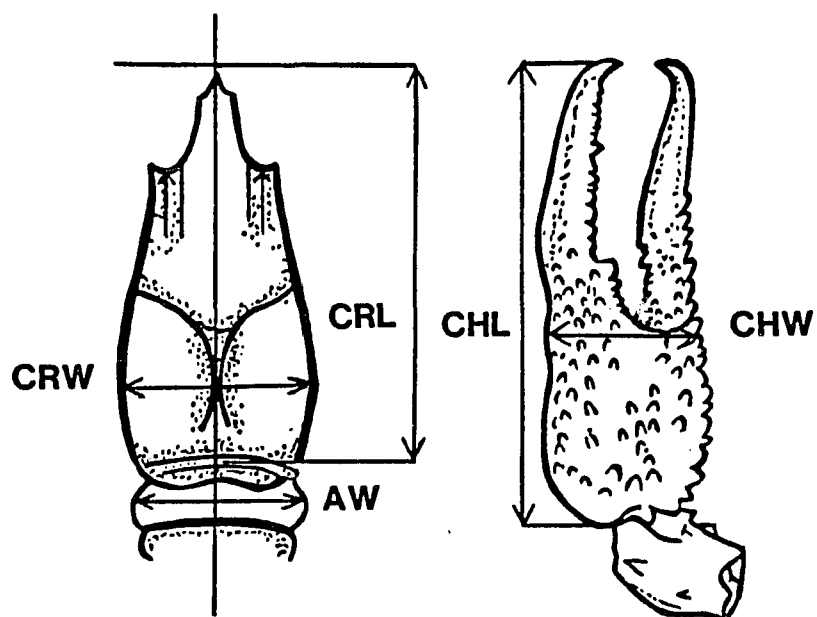
On 10 February and 15 March 1986, crawfish were sampled with 0.2-cm mesh plastic minnow traps to obtain an estimate of mean total length (tip of rostrum to posterior margin of telson). Estimates were compared to growth data from commercial, research, and wild populations of P. clarkii (Romaine 1976, O'Brien 1977, Lutz 1983) to predict the approximate date when the majority of the crawfish would

reach marketable size (≥ 75 mm total length).

After 150 days, pools were drained and crawfish from each full-sib family were harvested and maintained in separate 40-liter tanks. Crawfish were sorted by sex and male reproductive maturity and measured for chela length, chela width, carapace length (Fitzpatrick 1977), carapace width, abdomen width, abdomen depth, (Figure 1), total length, and total weight. Reproductively immature and mature female P. clarkii cannot be clearly differentiated solely on external characters (Lutz 1983); accordingly, females were not sorted by maturity. A number of crawfish from each full-sib family was selected to serve as broodstock for future studies; remaining crawfish were boiled in unseasoned water for 5 minutes (Craig 1985), and allowed to cool until safe to handle. Abdomen meat from each individual was removed in as consistent a manner as possible, following strictly the methods outlined by Moody (1980). Dressout percentage was calculated for each individual as the ratio of abdomen meat weight to total weight.

Differential survival within pools necessitated the adjustment of individual total length and weight for the density of crawfish in each pool at the time of harvest (Lutz and Wolters 1986, Craig 1985). Using density as a covariable, with length at harvest inversely related to density at harvest as documented by Lutz and Wolters (1986), all but a negligible portion of differences in total length and weight between pool environments as described by Craig (1985) were removed from the analysis.

Since the size at which growth ceases and sexual dimorphism is



CRW - Carapace Width
CRL - Carapace Length
AW - Abdomen Width

CHL - Chela Length
CHW - Chela Width

AD - Abdomen Depth

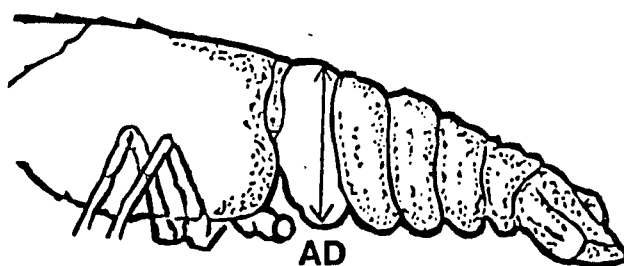


Figure 1. Body size traits measured on red swamp crawfish, Procambarus clarkii for estimation of heritabilities.

expressed in P. clarkii may be quite variable depending on environmental conditions (Huner and Romaine 1978), measurements of body size traits and abdomen meat weight were adjusted by regression for actual total length of individual crawfish in order to accurately describe heritabilities of relative sizes of various body parts. Dressout percentages were also adjusted by regression for total length of individual crawfish to account for possible differences in saturation of boiling water and ease of abdomen meat removal resulting from differences in overall size. The model used for the analyses was:

$$Y_{ijk} = u + B(X_{ijk} - \bar{X}) + S_i + D_{(i)j} + e_{ijk}$$

Y_{ijk} = measurement on the kth crawfish of the jth dam mated to the ith sire

u = population mean

B = slope of the regression of Y_{ijk} on density (for total length and weight) or on total length (for body size and processing traits)

X_{ijk} = density at harvest or total length of individual crawfish

\bar{X} = mean overall density or total length at harvest

S_i = effect of the ith sire

$D_{(i)j}$ = effect of the jth dam mated to the ith sire

e_{ijk} = residual error (assumed to be normally distributed with a mean of 0).

Sire (h^2_s), dam (h^2_d), and broad sense (h^2_{s+d}) heritabilities

were estimated for each trait for all animals combined and separately for females, reproductively mature (Form I) males (Word and Hobbs 1958), and reproductively immature (Form II and juvenile) males (Word and Hobbs 1958). Variance components associated with sire and

dam effects were estimated, after adjustment for the covariable of density or total length, with the VARCOMP procedure of the Statistical Analysis System (SAS) (Goodnight 1982) using the Type 1 sums of squares for random effects and the associated quadratics in a nested analysis of variance. Heritabilities and their standard errors were estimated from the correlation of half-sib families in an unbalanced nested design (Becker 1981, Falconer 1981).

RESULTS

Mating, Spawning, and Larval Survival

Successful oviposition resulted from 63 of 190 matings. Some females collected with advanced cement gland development died in mating tanks as a result of injuries presumably sustained during collection. In spite of successful oviposition, egg mortality was sufficiently high in some clutches to prevent their use in the analysis. All but 1 of the first 14 spawns were consumed by the females during a 1- to 2-week period, apparently as the result of frequent disturbance. Post-hatching losses of second- and third-instar larvae were consistently low.

From the 63 successful matings, only 41 represented 2 or more females mated to a common male. The earliest hatched of these full-sib families was discarded and one of the 40 selected full-sib families failed to produce a sufficient number of offspring for stocking; therefore, only 39 contemporaneous full-sib families were available for stocking into pools.

Growth and Survival

Growth rates averaged 2.1 mm per week from 29 November to 10 February, 7 mm per week from 10 February to 15 March, and 4 mm per week from 15 March to 1 May. Average growth rate for all animals over the study was 4 mm per week, and total length at harvest ranged from 54 mm to 114 mm.

Survival within pools ranged from 3% to 100% with a mean of 64%. A total of 747 animals was sexed and measured for total length at harvest, but, due to post-harvest mortality, only 635 survived to be included in the analysis of body size traits. Animals of various sizes died subsequent to harvest as the result of harvest-related injuries or molting and cannibalism while in the holding tanks.

Heritability Estimates

Sire heritabilities were not significantly different from 0 ($P > 0.05$) for any trait measured on all animals combined (Table I). Dam heritabilities for all animals combined were significant ($P < 0.05$) for total length, total weight, dressout percentage, abdomen meat weight, chela width, abdomen width, and carapace length. Estimates of dam heritabilities for carapace width, abdomen depth, and chela length were not significantly different from 0 ($P > 0.05$).

Significant ($P < 0.05$) broad sense heritabilities were estimated for all traits when all animals were combined (Table I). Estimates (\pm S.E.) ranged from 0.77 ± 0.19 for tail meat weight to 0.12 ± 0.05 for chela length (Table I). Heritabilities of two traits of economic importance, total length and dressout percentage, were highly

Table I. Estimates of heritabilities, their standard errors, and observed phenotypic coefficients of variation for all Procambarus clarkii combined

Trait	n	$h^2_s \pm \text{S.E.}$	$h^2_d \pm \text{S.E.}$	$h^2_{s+d} \pm \text{S.E.}$	C.V.
Carapace length	635	$-0.04 \pm .09$	$0.35 \pm .14^*$	$0.16 \pm .05^{**}$	3.5
Carapace width	635	$0.10 \pm .10$	$0.17 \pm .10$	$0.13 \pm .05^{**}$	5.6
Chela length	629	$0.09 \pm .09$	$0.14 \pm .09$	$0.12 \pm .05^*$	19.9
Chela width	630	$0.17 \pm .16$	$0.41 \pm .16^*$	$0.29 \pm .09^*$	19.4
Abdomen width	635	$0.04 \pm .12$	$0.41 \pm .16^*$	$0.22 \pm .07^{**}$	4.1
Abdomen depth	635	$0.18 \pm .13$	$0.19 \pm .10$	$0.18 \pm .09^{**}$	5.2
Abdomen meat wt.	333	$0.21 \pm .36$	$1.32 \pm .37^{**}$	$0.77 \pm .19^{**}$	13.7
Total weight	632	$0.01 \pm .17$	$-0.77 \pm .24^{**}$	$0.39 \pm .10^{**}$	43.5
Dressout percent.	331	$0.38 \pm .31$	$0.71 \pm .25^{**}$	$0.54 \pm .16^{**}$	21.3
Total length	635	$0.12 \pm .22$	$0.87 \pm .26^{**}$	$0.49 \pm .13^{**}$	10.9

*, ** P < 0.05, 0.01, significantly different from 0.00, respectively.

significant ($P < 0.01$).

For females, sire heritability estimates were not significant ($P > 0.05$) for any trait (Table II). Dam heritability estimates were significant ($P < 0.05$) for total length, total weight, dressout percentage, carapace width, carapace length, abdomen width, and chela width, while broad sense heritability estimates were significant ($P < 0.05$) for all traits except carapace length ($P < 0.07$).

No sire heritability estimates were significant for mature (Form I) males (Table III). Dam heritability estimates were significant ($P < 0.05$) for total length, total weight, abdomen meat weight, dressout percentage and chela width. Broad sense heritabilities of total length, total weight, carapace length, chela length, chela width, abdomen meat weight, and dressout percentage were also significant ($P < 0.05$).

Immature (Form II and juvenile) males comprised an extremely small sample for this type of analysis ($n=66$). In spite of the probability of unreasonable estimates under such conditions (Leone et al. 1968), sire heritability estimates were significant ($P < 0.05$) for carapace length and dressout percentage (Table IV). Although no dam heritability estimates were significant for immature males, broad sense heritabilities were significant ($P < 0.05$) for total length, total weight, dressout percentage, chela width, and chela length.

DISCUSSION

Husbandry Methods

Problems in maintaining and spawning female crawfish in this

Table II. Estimates of heritabilities, their standard errors, and observed phenotypic coefficients of variation for female Procambarus clarkii

Trait	n	$h^2_s \pm \text{S.E.}$	$h^2_d \pm \text{S.E.}$	$h^2_{s+d} \pm \text{S.E.}$	C.V.
Carapace length	342	$-0.15 \pm .11$	$0.45 \pm .22^*$	$0.15 \pm .08$	3.4
Carapace width	342	$0.35 \pm .27$	$0.53 \pm .23^*$	$0.44 \pm .14^{**}$	3.4
Chela length	341	$0.15 \pm .17$	$0.31 \pm .18$	$0.23 \pm .10^*$	11.0
Chela width	341	$0.29 \pm .26$	$0.59 \pm .24^*$	$0.44 \pm .14^{**}$	14.2
Abdomen width	342	$0.12 \pm .21$	$0.57 \pm .24^*$	$0.35 \pm .12^{**}$	3.1
Abdomen depth	342	$0.21 \pm .18$	$0.21 \pm .16$	$0.21 \pm .10^*$	5.2
Abdomen meat wt.	187	$0.22 \pm .40$	$1.27 \pm .42^{**}$	$0.75 \pm .21^{**}$	11.8
Total weight	342	$0.23 \pm .22$	$0.46 \pm .21^*$	$0.34 \pm .12^{**}$	40.3
Dressout percent.	187	$0.78 \pm .46$	$0.56 \pm .27^*$	$0.67 \pm .23^*$	15.1
Total length	342	$0.17 \pm .22$	$0.56 \pm .24^*$	$0.37 \pm .12^{**}$	10.7

*, ** P < 0.05, 0.01, significantly different from 0.00, respectively.

Table III. Estimates of heritabilities, their standard errors, and observed phenotypic coefficients of variation for mature (Form I) male Procambarus clarkii

Trait	n	$h^2_s \pm \text{S.E.}$	$h^2_d \pm \text{S.E.}$	$h^2_{s+d} \pm \text{S.E.}$	C.V.
Carapace length	230	$0.30 \pm .27$	$0.39 \pm .26$	$0.35 \pm .15^*$	3.1
Carapace width	230	$-0.22 \pm .10$	$0.19 \pm .25$	$-0.02 \pm .08$	6.7
Chela length	227	$0.40 \pm .32$	$0.56 \pm .30$	$0.48 \pm .18^{**}$	8.4
Chela width	228	$0.29 \pm .30$	$0.62 \pm .31^*$	$0.46 \pm .17^{**}$	10.0
Abdomen width	230	$-0.29 \pm .16$	$0.73 \pm .36^*$	$0.22 \pm .12$	3.9
Abdomen depth	230	$0.15 \pm .17$	$0.05 \pm .22$	$0.10 \pm .10$	4.8
Abdomen meat wt.	121	$0.47 \pm .66$	$1.73 \pm .62^{**}$	$1.10 \pm .33^{**}$	14.0
Total weight	228	$-0.02 \pm .24$	$0.85 \pm .38^*$	$0.41 \pm .16^*$	39.3
Dressout percent.	120	$0.08 \pm .48$	$1.24 \pm .56^*$	$0.66 \pm .23^*$	17.9
Total length	230	$0.34 \pm .33$	$0.71 \pm .33^*$	$0.53 \pm .18^{**}$	10.2

*,** P < 0.05, 0.01, significantly different from 0.00, respectively.

Table IV. Estimates of heritabilities, their standard errors, and observed phenotypic coefficients of variation for immature (Form II and juvenile) male Procambarus clarkii

Trait	n	$h^2_s \pm \text{S.E.}$	$h^2_d \pm \text{S.E.}$	$h^2_{s+d} \pm \text{S.E.}$	C.V.
Carapace length	63	$1.35 \pm .55^*$	$-1.35 \pm .17^{**}$	$0.00 \pm .32$	3.7
Carapace width	63	$0.27 \pm .32$	$-1.09 \pm .53$	$-0.41 \pm .25$	5.7
Chela length	61	$0.84 \pm .65$	$1.49 \pm .82$	$0.61 \pm .31^*$	12.2
Chela width	61	$0.18 \pm .69$	$1.25 \pm .75$	$0.71 \pm .34^*$	14.9
Abdomen width	63	$0.76 \pm .35$	$-1.61 \pm .45$	$-0.42 \pm .26$	5.7
Abdomen depth	63	$0.74 \pm .40$	$-1.27 \pm .47$	$-0.26 \pm .27$	5.1
Abdomen meat wt.	25	$1.73 \pm .97$	-2.12 ± 1.2	$-0.20 \pm .76$	14.4
Total weight	62	$-0.27 \pm .65$	$1.49 \pm .82$	$0.61 \pm .31$	44.1
Dressout percent.	24	$3.70 \pm .21^{**}$	$-0.14 \pm .14$	$1.78 \pm .12^{**}$	14.8
Total length	63	$-0.24 \pm .67$	$1.59 \pm .82$	$0.68 \pm .31^*$	12.3

*, ** P < 0.05, 0.01, significantly different from 0.00, respectively.

study may have resulted in part from disturbances related to regular feeding and checking for oviposition. Under natural conditions, females spawn in burrows that are usually capped with mud or deep enough to allow no outside disturbance (Konikoff 1977). Female crawfish may be reluctant to oviposit or maintain their eggs in the presence of regular disturbance.

Maintenance of third instar larvae over prolonged periods presented no problem in this study. This life stage has adapted to spending prolonged periods of time in brood burrows when conditions are not favorable for dispersal (Konikoff 1977).

Growth and Survival

Growth rates and survival in this study were generally higher than those reported in previous studies with P. clarkii in experimental pools during the same months of the year. Craig (1985) reported a mean growth rate of 3.6 mm per week and a mean survival of 41% for offspring from 15 families of crawfish raised for 175 days at an initial density of 6 per m² in experimental pools with rice as forage. Clark et al. (1974) reported a mean growth rate of approximately 2.8 mm per week and a mean survival of 68% for crawfish stocked as juveniles at 3 and 6 per m² in experimental pools.

Although initial stocking densities were the same as those used by Craig (1985), densities at harvest and growth rates were higher than those reported by Craig (1985). Although Clark et al. (1974) found no significant effect of density on growth or survival at 3 and 6 crawfish per m², Lutz and Wolters (1986) documented significant

effects of density on growth of P. clarkii in experimental pools, but no significant effect on survival. Temperature and dissolved oxygen levels throughout the study were comparable to those reported by Craig (1985), and ranged from 2 to 21 C and 6.0 to 15.0 ppm, respectively.

Substantial numbers of crawfish were lost to injuries sustained during and after harvesting. Most of these injuries were the result of molting and subsequent cannibalism or of punctures inflicted by crawfish on each other in pools, harvesting buckets, and holding tanks during harvesting. Smaller animals appeared to be somewhat more prone to such injuries.

Heritability Estimates

Heritability estimates for growth rate obtained in this study are comparable to those previously reported for other decapods. Hedgecock and Nelson (1978) estimated the upper limits of family heritability for growth in carapace length and wet weight in their population of lobsters (Homarus americanus) to be 0.28-0.34 and 0.26-0.50, respectively. In the freshwater prawn Macrobrachium rosenbergii, Malecha et al. (1984) reported heritabilities of juvenile growth in weight at 311 days post-metamorphosis to be 0.35 ± 0.15 for females and not significantly different from 0.00 for males, and suggested differences in heritabilities between sexes might be due to sex-linkage.

Negative heritability estimates, based on negative variance components, are often interpreted as representing values of 0.00 or very close to 0.00 as a result of the unbiased nature of ANOVA-based

variance component estimators (Thompson and Moore 1963). Dam heritability estimates are biased upwards by dominance, maternal, epistatic, and, in this case, common environmental effects. Broad sense estimates, being essentially the average of sire and dam estimates, are also inflated by such sources of bias (Becker 1981). Craig (1985) reported that after adjusting for density effects, resulting from varying survival, common pool environment consistently accounted for negligible portions of phenotypic variation in growth traits measured in this study. It is probable that addition of supplemental forage in the present study further reduced variation among pool environments from levels reported by Craig (1985).

Although most sire estimates in this study did not differ significantly from 0.00, large standard errors were not unexpected considering the relatively small sample size and small number of sires represented here (Becker 1981). In the case of estimates for immature males, it is possible that social interactions and dominance or maternal effects may have augmented discrepancies in some traits from the range of estimates expected from small sample sizes (Henderson 1986).

Potential Genetic Improvement

Although a trait may display high heritability, little genetic progress can be expected through selection in the absence of sufficient phenotypic variation. Traits in this study that described the size and shape of the carapace and abdomen displayed relatively little phenotypic variation, while the dimensions of the chelae appear

to be quite variable. Abdomen meat weight, dressout percentage, and total length all displayed moderately high phenotypic variability, and total weight displayed extremely high variation. These relationships were the same for all animals combined and for females, mature males, and immature males separately (Tables I-IV).

Total weight exhibits a higher degree of variability in crawfish than does total length under conditions such as encountered in this study due to variation in relative weight of the exoskeleton. This variation is the result of differences in rate of growth, state of maturity, water and soil hardness, and other factors (de la Bretonne and Avault 1971, Huner and Romaine 1978). Total length as measured in this study represents only one aspect of the growth pattern of crawfish, major components of which are the rate of growth and the size at which growth slows or ceases. At harvest, many males (75%) had already attained sexual maturity and had temporarily ceased growing. Many males that had not yet ceased to grow were relatively small; it was not clear whether the length at which they eventually would cease growing might be comparable to that of faster growing animals.

Stunted populations, in which crawfish reach maturity at sub-marketable sizes, are a common problem in crawfish culture. Producers currently harvest the fastest growing individuals during the course of the season, leaving generally slower growing animals remaining as broodstock to produce the next season's crop (Lutz 1983). Heritability estimates for growth in length and weight obtained in this study suggest that unintentional genetic selection in culture

ponds may result from this harvesting strategy. Such indirect selection for genetic change in aquaculture environments has been discussed by Doyle et al. (1983) using freshwater prawn culture to illustrate specific processes.

Dressout percentage is an important economic character in crawfish. Many smaller crawfish are not sold as a live product but are processed in peeling plants which market fresh and frozen abdomen meat. This market accounts for approximately 40% of the total harvest of crawfish in Louisiana (Dellenbarger et al. 1986). Dressout percentage could conceivably be changed by indirect selection on one or a combination of the body size traits measured here. Many factors, including sex, size, and maturity, affect dressout percentage in crawfish (Craig 1985). Sexual dimorphism of size and shape of the chela and abdomen has been described in several decapod species (Huxley 1932) and in cambarid and astacid crawfishes as a reflection of sexual maturity (Villalobos 1983, Stein et al. 1977, Rhodes and Holdich 1979). The size at which growth ceases and sexual dimorphism is expressed in P. clarkii may be quite variable depending on environmental conditions (Huner and Romaine 1978). As evidenced by the findings of Stein et al. (1977), these changes have a profound effect on dressout percentage. The extent to which this process might be partially controlled by hereditary factors is not well-defined for decapods in general.

Improvement of dressout percentage in crawfish through selection would necessitate at least moderate changes in the relative sizes of body parts. Carapace width and length, abdomen width and depth, and

chela width and length all appear to be heritable to some degree in P. clarkii. These traits may be of use in selection schemes which allow maximum selection for dressout percentage without the need for sacrificing large numbers of siblings to ascertain breeding values. Robertson (1962) suggested that under natural selection, various forces appeared to balance the relative size of appendages in male Drosophila around some optimum value, such as the negative relationship between wing area and courtship efficiency, and demonstrated that the relative size of appendages of the exoskeleton of his population of D. melanogaster could be easily altered through artificial selection. Stein (1976) demonstrated a similar situation in cambarid crawfish under natural selection, where chela size appears to directly effect the reproductive success of Form I males. In instances where they are in opposition to desired genetic change for crawfish under culture conditions, such forces of natural selection might be minimized through appropriate stock management practices.

CONCLUSIONS

All traits measured in this study appeared to show potential for at least moderate improvement through selection. Non-additive sources of variation, such as maternal, dominance, or common environmental effects were found to influence all traits measured. Data from this study suggest that the main economic traits of crawfish, growth in length and dressout percentage, with sire heritabilities for all animals combined of 0.12 ± 0.22 and 0.38 ± 0.31 , respectively, might best be improved through some means other than mass selection. Both

these traits exhibit sufficient phenotypic variation to allow for substantial selection pressure. Improvement of dressout percentage may also be possible through indirect selection using restricted selection indices to decrease or increase various body size traits, such as chela size. Techniques for spawning crawfish under laboratory conditions to produce full- and half-sib families were moderately successful and may be improved through minimizing disturbance of brood females.

STUDY II:

ESTIMATION OF GENETIC AND ENVIRONMENTAL CORRELATIONS AND FORMULATION OF SELECTION INDICES FOR GROWTH, BODY SIZE, AND PROCESSING TRAITS IN RED SWAMP CRAWFISH, PROCAMBARUS CLARKII (GIRARD)

ABSTRACT

Lutz, C.G., and W.R. Wolters, 1987. Estimation of genetic and environmental correlations and formulation of selection indices for growth, body size, and processing traits in red swamp crawfish, Procambarus clarkii (Girard).

Total length, total weight, carapace length, carapace width, abdomen width, abdomen depth, chela length, chela width, abdomen meat weight and dressout percentage were measured on individual crawfish (Procambarus clarkii (Girard)) from 39 full-sib families nested within 15 half-sib families. Crawfish were stocked as stage III juveniles at $6/m^2$ in 2.4 m diameter fiberglass pools planted with rice (Oryza sativa) for forage. Total length and weight were adjusted for the effect of density within pools as the result of differential survival; other traits were adjusted for total length. Analysis of adjusted traits was performed using a mixed model, yielding BLUE's (Best Linear Unbiased Estimators) of the fixed effects of sex and male maturity, Henderson's Method III variance and covariance components, and sire, dam, and sire + dam genetic and environmental correlations based on these components. Heritability estimates based on Method III variance component estimates were generally in good agreement with previously

reported estimates derived from traditional ANOVA-based variance components. Estimates of genetic correlations were utilized to formulate a selection index to maximize genetic improvement in net economic worth, based on industry-wide utilization of whole crawfish and processed abdomen meat. Selection indices were also formulated to maximize improvement in growth or dressout percentage individually. Selection index weights showed that if substantial genetic gains are possible in the two major economic aspects of crawfish culture, growth and processing traits, they can be realized simultaneously in selection programs.

INTRODUCTION

Agricultural production of Procambarid crawfishes currently occupies over 50,000 ha in the U.S., with 1985-86 yields approaching 27 million kg (Louisiana Cooperative Extension Service 1986). Red swamp crawfish, Procambarus clarkii, comprise the bulk of the commercial and wild harvest of crawfish in the U.S., and historically accounts for approximately 90% of yields in Louisiana. Cultured P. clarkii stocks are often only several generations removed from wild seed stock, and producers and researchers have recently expressed interest in the potential for genetic improvement in this species, especially through selection. Recent research has provided substantial information regarding genetic and environmental effects on phenotypic expression of growth, processing, and specific body size traits (Craig 1985, Lutz and Wolters 1986, Lutz and Wolters 1988).

Knowledge of genetic correlations between traits and the relative

economic value of each trait is essential prior to formulating selection indices which will result in the greatest economic improvement in P. clarkii. Dobzhansky (1937) was one of the first to point out that "most, and possibly all, genes have manifold effects", and Hazel (1943) cautioned that genetic correlations between desirable traits "make wise selection a complicated and uncertain procedure." Genes having a favorable effect on one trait may have the opposite effect on another trait the breeder wishes to improve, yielding negative genetic correlations; a common example is milk yield and percent milkfat in dairy cattle (Touchberry 1963).

Growth rate has substantial importance in commercial crawfish culture in terms of seasonal trends in the value of harvested animals and in relation to emerging marketing trends of grading yields into several size groups. Approximately 40% of the crawfish harvest in Louisiana is processed as peeled abdominal meat; accordingly, dressout percentage is an important economic trait in P. clarkii. This study was undertaken to provide estimates of genetic and environmental correlations for growth, body size, and processing traits in P. clarkii, and to formulate selection indices to maximize genetic improvement in overall economic value, growth in total length, and dressout percentage.

MATERIALS AND METHODS

A total of 752 crawfish (P. clarkii) from 39 full-sib families nested within 15 half-sib families was raised for 150 days in fiberglass pools, harvested, sorted by sex and male reproductive

maturity, and measured for chela length, chela width, carapace length (Fitzpatrick 1977), carapace width, abdomen depth, (Figure 1) total length, total weight, abdomen meat weight and dressout percentage (Lutz and Wolters 1988).

Differential survival to harvest among pools necessitated the adjustment of individual total length and weight for the density of crawfish in each pool at the time of harvest (Lutz and Wolters 1986). Measurements of body size traits were adjusted for total length of individual crawfish in order to accurately describe variances and covariances of relative sizes of various body parts (Lutz and Wolters 1988). Adjusted traits were used in a mixed model computer analysis (LSMLMW) (Harvey 1985) to determine the significance of the fixed effects of sex and male maturity on each trait and to estimate Henderson's Method III sire, dam, and error variances and covariances (Henderson 1953) to provide estimates of genetic and environmental correlations. The model used for the analyses was:

$$Y_{ijkl} = u + B(X_{ijkl} - \bar{X}) + S_i + D_{(i)j} + F_k + e_{ijkl}$$

Y_{ijkl} = measurement on the l th crawfish of the k th sex (or state of male maturity) from the j th dam mated to the i th sire

u = population mean

B = slope of the regression of Y_{ijkl} on density (for total length and weight) or on total length (for body size traits)

X_{ijkl} = density at harvest or total length of individual crawfish

\bar{X} = mean overall density or total length at harvest

S_i = effect of the i th sire (Random)

$D_{(i)j}$ = effect of the j th dam mated to the i th sire (Random)

F_k = effect of sex or state of male maturity (Fixed)

e_{ijk} = residual error (assumed to be normally distributed with a mean of 0).

Phenotypic correlations (r_p), sire (s), dam (d), and broad sense (sire + dam) genetic (r_G) and environmental (r_E) correlations, standard errors of genetic correlations, and BLUE's (Best Linear Unbiased Estimators) of fixed effects were computed using equations for unbalanced designs (Harvey 1960, 1964). Sire (h^2_s), dam (h^2_d) and broad sense (h^2_{s+d}) heritability estimates for all animals combined were derived from Method III variance components. These estimates were compared to previously reported heritability estimates for the same population (Lutz and Wolters 1988), which were derived from traditional ANOVA-based variance components (Becker 1981).

A genetic correlation matrix was constructed from sire correlation estimates of traits measured on all animals. In instances where correlation estimates fell outside of the theoretical parameter range or were non-estimable, estimates were initially set to ± 1.00 or 0.00, respectively. Eigenvalues of the correlation matrix were subsequently derived to determine if the matrix was positive definite. To ensure conservative estimates of gains based on selection indices, correlation estimates set to 1.00 were then reduced by 0.01 until the correlation matrix was positive definite or the 95% confidence limit of each correlation estimate was reached. Since processing traits were measured on a non-random sample, these traits were not included in the matrix from which eigenvalues were to be derived.

Genetic (sire) and phenotypic correlation matrices were used to

formulate a selection index to maximize genetic improvement in net economic worth of individual crawfish. Economic weights were assigned to total length, total weight, abdomen meat weight, and dressout percentage traits based on the average portion of industry yields marketed as peeled abdominal meat and that marketed as whole, live animals (Dellenbarger et al. 1986). Processing traits and growth traits were assigned values of 0.42 and 0.58, respectively. Two additional selection indices, maximizing genetic gains in growth traits and processing traits separately, were formulated in the same manner. A non-symmetric matrix of genetic correlation estimates, including abdomen meat weight and dressout percentage, was utilized. This matrix was non-symmetric due to the inability to obtain measurements of these traits on animals to be saved for selection programs. Genetic correlation estimates for abdomen meat weight and dressout percentage were set to 1.00 or their 95% confidence limits in the same manner as were traits measured on all animals. Changes in other body size traits were considered inconsequential and assigned weights of 0.00.

RESULTS

Variance, Covariance and Correlation estimates

Sire genetic correlation estimates were significant ($P < 0.05$) for total length with chela length, chela width, total weight, abdomen meat weight, and dressout percentage, for abdomen depth with abdomen meat weight and dressout percentage, for chela length with chela width, total weight, abdomen meat weight, and dressout percentage, for

chela width with total weight, abdomen meat weight, and dressout percentage, and for abdomen meat weight with dressout percentage (Table I). Sire genetic correlations were non-estimable in some instances, as the result of setting negative sire variance component estimates equal to 0. Sire genetic correlation estimates generally fell within the theoretical parameter range for correlations. In all instances, 95% confidence limits of sire estimates fell within the theoretical parameter range.

Dam genetic correlation estimates were significant ($P < 0.05$) for total length with abdomen depth, chela length, and total weight, for carapace width with chela width, for abdomen depth with abdomen width, chela length, chela width, and total weight, for abdomen width with abdomen meat weight, for chela length with chela width and total weight, and for abdomen meat weight with dressout percentage (Table I). Sire + dam genetic correlation estimates were significant ($P < 0.05$) for total length with abdomen depth, chela length, chela width, and total weight, for carapace width with chela width, for abdomen depth with chela length, chela width, total weight, abdomen meat weight, and dressout percentage, for chela length with chela width, total weight, and dressout percentage, for chela width with total weight and dressout percentage, and for abdomen meat weight with dressout percentage (Table I). Dam and sire + dam correlation estimates consistently fell within the theoretical parameter range.

Sire, dam, and sire + dam environmental correlation estimates were of opposing sign to genetic correlation estimates in some instances. Dominance and/or epistatic effects occasionally resulted

Table I. Phenotypic, genetic (\pm S.E.'s) and environmental correlations for adjusted body size traits in Procambarus clarkii 150 days post-stocking.

Trait 1	Trait 2	r_p	r_{Gs}	r_{Gd}	r_{Gs+d}	r_{Es}	r_{Ed}	r_{Es+d}
Total Length	Carapace Width	-0.02	1.23 (.68)	-0.33 (.43)	-0.03 (.35)	-0.11	0.06	-0.03
Total Length	Carapace Length	-0.03	N.E. ^a	-0.05 (.35)	-0.25 (.31)	N.E.	-0.02	0.02
Total Length	Abdomen Depth	-0.08	0.49 (.40)	0.90* (.41)	0.71* (.23)	-0.18	-0.33	-0.25
Total Length	Abdomen Width	-0.08	-1.74 (1.32)	0.30 (.35)	0.02 (.31)	0.01	-0.27	-0.10
Total Length	Chela Length	-0.05	-1.01** (.28)	-0.83* (.31)	-0.89** (.16)	0.10	0.26	0.17
Total Length	Chela Width	-0.03	-1.21** (.22)	-0.50 (.30)	-0.71** (.19)	0.21	0.33	0.25
Total Length	Total Weight	0.93	1.12** (.14)	0.95** (.05)	0.98** (.03)	0.92	0.93	0.93
Total Length	Abdomen Meat Wt.	-0.12	1.65** (.57)	-0.06 (.26)	0.15 (.26)	-0.49	-0.29	-0.92
Total Length	Dressout Percent.	-0.07	1.73** (.56)	-0.14 (.30)	0.30 (.26)	-0.98	-0.36	-0.71
Carapace Width	Carapace Length	0.14	N.E.	0.22 (.36)	0.28 (.32)	N.E.	0.11	0.12
Carapace Width	Abdomen Depth	0.11	0.50 (.56)	-0.12 (.46)	0.07 (.34)	0.07	0.16	0.12
Carapace Width	Abdomen Width	0.47	-3.46 (4.38)	0.41 (.31)	0.06 (.33)	0.59	0.52	0.56
Carapace Width	Chela Length	0.41	-0.28 (.57)	0.39 (.33)	0.23 (.31)	0.48	0.42	0.45
Carapace Width	Chela Width	0.42	-0.02 (.60)	0.73** (.22)	0.57* (.22)	0.50	0.30	0.42

a: Non-estimable

*, **, P < 0.05, 0.01 significantly different from 0.00

Table I. Continued

Trait 1	Trait 2	r_P	r_{Gs}	r_{Gd}	r_{Gs+d}	r_{Es}	r_{Ed}	r_{Es+d}
Carapace Width	Total Weight	0.13	1.83 (1.06)	-0.25 (.43)	0.10 (.37)	0.05	0.23	0.13
Carapace Width	Abdomen Meat Wt.	0.08	N.E.	0.06 (.28)	-0.06 (.28)	N.E.	-0.03	0.37
Carapace Width	Dressout Percent.	-0.48	N.E.	-0.63 (.33)	-0.38 (.28)	N.E.	-0.05	-0.64
Carapace Length	Abdomen Depth	-0.01	N.E.	-0.06 (.39)	-0.18 (.30)	N.E.	0.02	0.04
Carapace Length	Abdomen Width	0.04	N.E.	-0.03 (.31)	0.22 (.29)	N.E.	0.10	-0.01
Carapace Length	Chela Length	0.24	N.E.	0.12 (.32)	0.27 (.28)	N.E.	0.32	0.24
Carapace Length	Chela Width	0.22	N.E.	-0.03 (.29)	0.22 (.27)	N.E.	0.54	0.24
Carapace Length	Total Weight	0.04	N.E.	-0.14 (.37)	-0.26 (.32)	N.E.	0.12	0.10
Carapace Length	Abdomen Meat Wt.	-0.18	N.E.	0.04 (.26)	-0.27 (.25)	N.E.	-0.76	0.07
Carapace Length	Dressout Percent.	-0.31	N.E.	-0.13 (.30)	-0.44 (.24)	N.E.	0.84	-0.09
Abdomen Depth	Abdomen Width	0.21	-1.03 (.74)	0.75** (.28)	0.32 (.28)	0.32	-0.02	0.17
Abdomen Depth	Chela Length	-0.09	-0.17 (.40)	-1.16** (.33)	-0.72** (.21)	-0.07	0.28	0.10
Abdomen Depth	Chela Width	-0.08	-0.36 (.35)	-0.67* (.32)	-0.53* (.23)	0.00	0.27	0.12
Abdomen Depth	Total Weight	-0.03	0.54 (.53)	0.89* (.41)	0.71** (.25)	-0.09	-0.25	-0.17
Abdomen Depth	Abdomen Meat Wt.	0.46	1.10** (.14)	0.59 (.31)	0.67** (.19)	0.26	-0.21	0.49
Abdomen Depth	Dressout Percent	0.24	1.02** (.15)	0.75 (.38)	0.88** (.15)	-0.30	-0.10	-0.21

Table I. Continued

Trait 1	Trait 2	r_p	r_{Gs}	r_{Gd}	r_{Gs+d}	r_{Es}	r_{Ed}	r_{Es+d}
Abdomen Width	Chela Length	0.21	0.93 (.73)	-0.27 (.30)	-0.09 (.29)	0.16	0.52	0.30
Abdomen Width	Total Weight	0.02	-1.99 (1.63)	0.34 (.35)	0.11 (.33)	0.09	-0.12	0.01
Abdomen Width	Abdomen Meat Wt.	0.34	N.E.	0.56* (.23)	0.38 (.26)	N.E.	0.38	0.49
Abdomen Width	Dressout Percent.	-0.16	N.E.	-0.07 (.35)	-0.02 (.30)	N.E.	-0.35	-0.32
Chela Length	Chela Width	0.89	0.93** (.06)	0.88** (.07)	0.89** (.06)	0.88	0.98	0.91
Chela Length	Total Weight	0.20	-1.07** (.40)	-0.91** (.25)	-0.93** (.14)	0.34	0.63	0.47
Chela Length	Abdomen Meat Wt.	-0.22	-1.71** (.45)	-0.06 (.35)	-0.47 (.25)	0.34	0.32	0.11
Chela Length	Dressout Percent.	-0.70	-0.78** (.24)	-0.54 (.51)	-0.78** (.24)	-0.70	-0.99	-0.71
Chela Width	Abdomen Width	0.26	0.13 (.69)	0.24 (.27)	0.21 (.27)	0.27	0.30	0.29
Chela Width	Total Weight	0.21	-1.33** (.43)	-0.43 (.30)	-0.62** (.22)	0.41	0.71	0.52
Chela Width	Abdomen Meat Wt.	-0.23	-2.26* (.94)	-0.06 (.34)	-0.37 (.24)	0.52	0.32	0.16
Chela Width	Dressout Percent.	-0.75	-1.17** (.25)	-0.63 (.36)	-0.80** (.19)	-0.44	-1.33	-0.67
Abdomen Meat Wt.	Total Weight	-0.10	1.38 (2.56)	0.02 (.27)	0.09 (.27)	-0.22	-0.60	-4.05
Abdomen Meat Wt.	Dressout Percent.	0.62	1.40** (.26)	0.66** (.16)	0.80** (.10)	0.18	0.16	0.09
Total Weight	Dressout Percent	-0.25	3.26 (5.83)	-0.20 (.31)	0.17 (.27)	-1.01	3.27	-0.86

in sire, dam, and sire + dam environmental correlations of opposing sign (Table I). Sire environmental correlations were non-estimable in some instances, as the result of negative sire variance component estimates (Table I).

Mixed model heritability estimates

Heritability estimates derived from Henderson's Method III variance components were in agreement with previously reported estimates (Lutz and Wolters 1988) derived from ANOVA-based quadratics (Table II). One notable difference was the larger, significant ($P < 0.05$) sire heritability for dressout percentage based on Method III variance components.

Fixed effects

BLUE's of the fixed effects of sex and male maturity demonstrated differences between females, mature males, and immature males for specific individual traits (Table III). Females had larger abdomen dimensions and higher processing values than males, and exceeded the population mean in total length, although not in total weight. Mature males had larger carapaces, larger chelae, and smaller abdomens than females, and exceeded the population mean in both total length and total weight. Immature males had intermediate values for body size traits, and were smaller than the population mean in both total length and weight.

Table II. Comparison of heritability estimates, including standard errors, using ANOVA-based quadratics (Becker 1981) and Henderson's mixed model Method III quadratics (Henderson 1953) for growth, body size, and processing traits in Procambarus clarkii.

Trait	ANOVA			Method III		
	h^2_s	h^2_d	h^2_{s+d}	h^2_s	h^2_d	h^2_{s+d}
Total Length	0.12 (.22)	0.87** (.26)	0.49** (.13)	0.11 (.08)	0.23* (.11)	0.17* (.07)
Carapace Width	0.10 (.10)	0.17 (.10)	0.13** (.05)	0.04 (.05)	0.20* (.10)	0.12* (.06)
Carapace Length	-0.04 (.09)	0.35* (.14)	0.16** (.05)	0.00 (N.E. ^a)	0.44** (.14)	0.22** (.08)
Abdomen Depth	0.18 (.13)	0.19 (.10)	0.18* (.09)	0.22 (.11)	0.18 (.10)	0.20** (.07)
Abdomen Width	0.04 (.12)	0.41* (.16)	0.22** (.07)	0.02 (.05)	0.46* (.14)	0.24** (.08)
Chela Length	0.09 (.09)	0.14 (.09)	0.12* (.05)	0.17 (.10)	0.35** (.13)	0.26** (.09)
Chela Width	0.17 (.16)	0.41* (.16)	0.29* (.09)	0.24 (.12)	0.65** (.17)	0.45** (.12)
Total Weight	0.01 (.17)	0.77** (.24)	0.39** (.10)	0.05 (.05)	0.21* (.10)	0.13* (.06)
Abdomen Meat Weight	0.21 (.36)	1.32** (.37)	0.77** (.19)	0.23 (.15)	1.49** (.27)	0.86** (.17)
Dressout %	0.38 (.31)	0.71** (.25)	0.54** (.16)	0.62* (.27)	0.72** (.22)	0.67** (.16)

a: Non-estimable

*,** P < 0.05, 0.01, significantly different from 0.00.

Table III. Best Linear Unbiased Estimates and significance levels of the fixed effects of sex and male reproductive maturity on growth, body size, and processing traits in Procambarus clarkii

<u>Trait</u>	<u>Mean</u>	<u>Females</u>	<u>Fixed Effect Levels</u>	
			<u>Males</u>	
			<u>Mature</u>	<u>Immature</u>
Total Length (mm)	88.558	0.263	1.506*	-1.769*
Carapace Width (mm)	20.275	-0.208**	0.599**	-0.392**
Carapace Length (mm)	47.374	-0.651**	0.652**	0.000
Abdomen Depth (mm)	12.157	0.171**	-0.121**	-0.050
Abdomen Width (mm)	17.531	0.391**	-0.068	-0.323**
Chela Length (mm)	35.023	-4.552**	8.067**	-3.515**
Chela Width (mm)	12.411	-0.902**	2.558**	-1.656**
Total Weight (g)	24.159	-1.358*	5.256**	-3.898**
Abdomen Meat Weight (g)	4.234	0.158**	-0.260**	0.102*
Dressout Percentage	19.3	1.4**	-3.9**	2.5**

*, ** : P < 0.05, 0.01, respectively.

Selection indices

The genetic correlation matrix including out of range estimates set to 1.00 yielded three negative eigenvalues, totalling -14.8% of total variation. Subsequent to setting all out of range estimates to their 95% confidence limits, the genetic correlation matrix yielded only one negative eigenvalue equal to -3.7% of total variation. Selection indices to maximize overall economic value, growth, and dressout percentage yielded differing weights for selection on body size traits (Table IV). Total length and total weight were consistently of opposite sign in all three indices; signs and magnitudes of weights of other traits were variable.

DISCUSSION

Covariance and correlation estimates

Falconer (1981) stated that genetic correlation estimates are subject to large sampling errors, are influenced by gene frequencies, and lack a great degree of precision. Although the nested mating design utilized in this study would be expected to minimize sampling error, limitations of space on the number of half-sib families available for the analysis probably contributed to sampling errors, and resulted in many sire correlation estimates which were non-estimable or outside the theoretical parameter range. Negative variance component estimates were the result of the unbiased nature of Henderson's Method III estimation procedure (Henderson 1953), and may have been due to small sample sizes. Out-of-range estimates and non-estimable correlations may also have been due to unquantifiable

Table IV. Selection index weights for growth and body size traits to maximize genetic improvement in net economic value, growth in length and weight, and processing traits in Procambarus clarkii

Trait	<u>Selection Index Weights</u>		
	Net Value	Growth	Processing Traits
Total Length (mm)	44.1	-9.1	53.2
Carapace Width (mm)	4.8	0.9	4.0
Carapace Length (mm)	3.0	1.1	1.9
Abdomen Depth (mm)	14.1	4.8	9.3
Abdomen Width (mm)	0.3	0.8	-0.5
Chela Length (mm)	4.1	8.4	-4.4
Chela Width (mm)	-9.4	-20.0	10.6
Total Weight (g)	-29.5	21.6	-51.1

negative covariances within families from competition or social interactions (Henderson 1986).

In some instances, genetic and environmental correlations were of opposing sign. Such situations have long been recognized in certain poultry, sheep and dairy cattle traits (Lerner and Cruden 1948, Morley 1951, Searle 1961). In most instances, effects of dominance and epistatic effects on differences among genetic and environmental correlation estimates were consistent. Inconsistencies in the interpretation of dominance and epistatic covariances as well as cases of sire correlation estimates outside of the theoretical parameter range appeared associated with correlations including processing traits and/or total weight. Substantial sampling error was probably associated with processing traits due to unavoidable inconsistency in manual removal of abdominal tail meat. Variation in exoskeleton contribution to total weight due to molt stage and variable amounts of calcium deposition associated with environmental variables such as water and soil hardness almost certainly contributed to sampling error of total weight.

Fixed effects

Differences in body size traits between females, mature males, and immature males were consistent with those reported in other studies (Stein et al. 1977, Craig 1985, Lutz et al. 1987). Low standard errors of genetic covariances after removing fixed effects suggest that sex linkage effects were generally low. Similar trends in total weight values and dimensions of the carapace and chelae were

partially the result of heavy calcium deposition in these regions of the exoskeleton (Chaisemartin 1962).

Selection indices

Index weights for total length and total weight were consistently of opposite sign in all three indices. Considering the high genetic correlation for these traits and their phenotypic relationship, it becomes necessary to consider their weights together when interpreting selection indices derived from these data. The index maximizing gains in net economic value and that maximizing growth should both result in an increase in overall size, while the index maximizing gains in processing traits should result in a negligible increase in growth. Index weights imply that genetic gains in growth and processing traits can be realized simultaneously; or, at the least, progress can be made in one area without losses in the other. Genetic correlation estimates used in these indices lacked precision as evidenced by the slight negative variance accounted for in the eigenvalues of the genetic correlation matrix. Results from larger data bases in the future should allow for an improved understanding of genetic relationships between growth, body size and processing traits.

CONCLUSIONS

Genetic correlation estimates obtained in this study lacked precision due to limited sample size. Female, mature male, and immature male levels of fixed effects for individual growth, body

size, and processing traits were consistent with previous studies. Genetic correlation estimates and resulting selection index weights suggest that genetic gains in the two major economic aspects of crawfish culture, growth and processing traits, are not mutually exclusive, but can be pursued simultaneously in future selection programs.

STUDY III:
RESPONSE TO SELECTION FOR GROWTH AND CORRELATED RESPONSE IN DRESSOUT
PERCENTAGE IN RED SWAMP CRAWFISH, PROCAMBARUS CLARKII (GIRARD)

ABSTRACT

Lutz, C.G., and W.R. Wolters, 1987. Response to selection for growth and correlated response in dressout percentage in red swamp crawfish, Procambarus clarkii (Girard).

Procambarus clarkii broodstock were selected from 39 full-sib families in family selection and 5 replicates of mass selection for growth in total length. Only one-way positive and negative family selection and three replicates of mass selection produced sufficient offspring to determine selection responses. Offspring were stocked into 2-3 replicate pools per line. Differences between lines in length and weight at harvest and in dressout percentage were analyzed within replicates of mass and family selection. In spite of moderate to high selection intensity in parental lines (0.74 to 4.57), no response to selection for growth in length or weight or correlated response in dressout percentage was found in either family or mass selection. These data imply little additive genetic control over growth traits in P. clarkii.

INTRODUCTION

Yields of extensively cultured Procambarid crawfish approached 27 million kg in the U.S. during the 1985-1986 season (Louisiana Cooperative Extension Service 1986). Agricultural production of crawfish is currently practiced on over 50,000 ha in the U.S., and expansion of the industry is expected to continue (Louisiana Cooperative Extension Service 1986). Louisiana accounts for the vast majority of the commercial crawfish harvest, and red swamp crawfish, Procambarus clarkii, is the major species cultured. Growth rate and processing traits have been identified as the major areas in which genetic improvement of P. clarkii would be most profitable (Lutz and Wolters 1987).

Producers and researchers have speculated that current harvesting strategies in commercial ponds may serve as a form of negative selection for growth. Crawfish are generally harvested with wire-mesh traps which retain animals at a specific minimum size (approximately 75 mm), resulting in early harvest of faster growing animals and the survival of slower growing animals to remain as broodstock in ponds to produce the next season's crop. Evidence of such selection would be difficult to discern in most commercial ponds due to the prolonged period of reproduction of P. clarkii under culture conditions (Lutz 1983) and environmental variability from one commercial season to the next. Environmental variability in forage type and abundance, population density, temperature, time of flooding, recruitment patterns, and other factors all effect growth and yield of

P. clarkii in commercial ponds (Lutz 1983, Lutz and Wolters 1986, Araujo-Leal 1986).

Although heritability estimates and genetic correlations for growth, body size and processing traits in P. clarkii have been determined from sib analysis (Lutz and Wolters 1987, 1988), these estimates had large standard errors, and may have been biased due to competition and social interactions within full-sib families in common environments (Falconer 1981, Henderson 1986). Processing and growth traits in P. clarkii had low heritabilities, but positive genetic correlations. Genetic gains in one group of traits would be expected to result in gains in the other group as well (Lutz and Wolters 1987). This study was undertaken to determine the response to selection for growth traits and correlated response of dressout percentage in P. clarkii after one generation of family selection and mass selection.

MATERIALS AND METHODS

Broodstock for Family Selection

Broodstock for family and mass selection were obtained from 39 full-sib families nested within 15 half-sib families, raised from third-instar larvae in fiberglass pools for 150 days with rice (Oryza sativa) as forage (Lutz and Wolters 1988). One male and one female were selected at random from each full-sib family to provide a control population for family selection. This control population was randomly divided into three replicates of approximately equal size.

Total length at harvest of individual crawfish was adjusted for

density at harvest due to differential survival within pools (Lutz and Wolters 1986). Full-sib families were subsequently ranked by mean total length. The 5 highest-ranked and 5 lowest-ranked families were selected to form positive and negative selected lines. Three males and 3 females were selected randomly from each of the 5 highest-ranked families. One male and one female from each family was assigned to one of 3 replicates within the positive selected line, so that within each replicate, each family was equally represented. Three replicates within the negative selected line were developed from the 5 lowest-ranked families in the same manner. Selection differentials and selection intensities were calculated based on the distribution of full-sib family means and the mean values of families selected to form positive and negative lines.

Broodstock for Mass Selection

A total of 27 remaining full-sib families was available to produce sufficient numbers of mass-selection broodstock subsequent to family selection. These families were randomly assigned to 5 replicate base populations comprised of 6, 6, 6, 5, and 4 full-sib families each. Within each base population, one male and one female from each family were randomly selected to form a control line. Positive and negative selected lines of equal number were formed from individuals remaining within each base population. Animals were assigned to positive and negative selected lines based solely on adjusted total length, regardless of full-sib or half-sib family of origin. All selected and control lines were comprised of equal

numbers of males and females. Annuli ventrales of selected females were cleansed with 95% ethanol and abrasive scouring pads to remove any previously acquired spermatophores (Berrill 1985), and ensure mating only within selected lines. Selection differentials within mass selection replicates were calculated for both sexes and subsequently averaged (Falconer 1981).

Maintenance of Broodstock

Each replicate within positive, negative, and control family selection lines was stocked at the time of selection into a separate 6.0-m diameter fiberglass tank. Prior to stocking, tanks were filled with soil to an average depth of 10 cm, and soil sloped up one side of each tank to allow crawfish to burrow above the water level. Standing water was maintained at a depth of 20 cm in the low end of each tank, and emergent vegetation such as alligatorweed (Philoxeroides sp.), smartweed (Polygonum sp.), and water primrose (Jussiaea sp.) was planted to provide forage and cover. Crawfish were fed a pelleted sinking catfish ration at 100 g per week to supplement natural foods. Tanks were supplied with continuous diffuse aeration at 0.30 m^3 per minute. Animals were allowed to mate randomly within tanks.

Each line within the 5 replicates of mass selection was stocked into a separate 2.4-m diameter pool with soil, standing water, and emergent vegetation as described for the 6.0-m tanks, and fed pelleted fish ration at 50 g per week. Pools were supplied with continuous diffuse aeration at 0.15 m^3 per minute. Animals within each mass selection line were allowed to mate at random.

Collection, Stocking and Grow-out of Offspring

On 2 September 1986, mass selection populations were removed from the fiberglass pools and maintained in partitioned 40-liter polyethylene tanks. Tanks containing females were covered with black plastic to minimize disturbance, and females monitored at 3- to 4-day intervals for oviposition or molting. Females which lost previously acquired spermatophores by molting were re-mated in random order to all surviving males within each line.

On 17 October 1986, family selection broodstock and offspring present were removed from the 6.0-m tanks. Due to poor survival of broodstock and delayed spawning in some tanks, replicates within family selection lines were pooled to provide sufficient numbers of offspring for stocking. Two samples of juvenile offspring from positive and control lines were stocked at 6 per m² into separate 2.4-m diameter pools planted with rice. Females were classified as reproductively active if they exhibited advanced cement gland development or attached eggs. These females were maintained in partitioned 40-liter polyethylene tanks covered with black plastic. On 19 November 1986, when third-instar larvae representing 5 or more females were available from negative and control family lines, 3 samples of offspring per line were stocked at 6 per m² into separate 2.4-m diameter pools planted with rice.

From 3 December 1986 to 29 January 1987, when a sufficient number of third-instar larvae representing 2 or more females from each line became available within a replicate of mass selection, offspring in each line were pooled and three samples per line were stocked at 6 per

m² into separate 2.4-m diameter pools planted with rice.

Data collection and analysis

From 7 November 1986 until 24 May 1987, pools were sampled periodically with 0.2 cm mesh plastic minnow traps to monitor growth in total length. Crawfish were maintained in pools until the majority of sampled animals in a selection replicate reached marketable size (≥ 75 mm total length) or males began to attain sexual maturity (Form I) (Word and Hobbs 1958). Within each replicate of selection, all pools were harvested on the same day.

At harvest, individual crawfish were sorted by sex and state of male maturity, weighed, and measured for total length. Crawfish from negative family selection and from all replicates of mass selection were boiled in unseasoned water for 5 minutes. Abdominal meat from each animal was removed and weighed to assess processing traits (Craig 1985). Differences between lines in total length and weight were analyzed in a one-way ANOVA using density at harvest as a covariable when significant ($P < 0.05$). Pool effects were used to test differences between lines when significant ($P < 0.05$).

RESULTS

Phenotypic variation and intensity of selection

Full-sib families had sufficient variation in mean adjusted total length to allow for only moderate selection intensity (Table I). Mass selection replicates had sufficient phenotypic variation to allow for high selection intensities (Table I). A higher selection intensity

Table I. Selection differentials (S.D.) and selection intensities (S.I. = S.D./population phenotypic standard deviation) obtained on Procambarus clarkii broodstock in family and replicated mass selection for density-adjusted total length (T.L.) (mm)

Trial	<u>Males</u>			<u>Females</u>			<u>Line Average</u>		
	T.L.	S.D.	S.I.	T.L.	S.D.	S.I.	T.L.	S.D.	S.I.
<u>Positive Family Selection</u>	-----	-----	-----	-----	-----	-----	97.1	8.3	1.16
<u>Negative Family Selection</u>	-----	-----	-----	-----	-----	-----	83.5	-5.3	-0.74
<u>Mass Selection</u>									
<u>Trial 1</u>									
Positive	100.8	12.0	2.01	95.8	7.1	0.83	98.3	9.6	1.42
Negative	75.4	-13.4	-2.24	74.4	-14.4	-1.70	74.9	-13.9	-1.97
<u>Trial 2</u>									
Positive	103.1	14.3	3.07	102.9	14.5	2.04	103.0	14.4	2.56
Negative	75.6	-13.2	-2.84	71.2	-17.3	-2.43	73.4	-15.3	-2.64
<u>Trial 3</u>									
Positive	106.9	18.1	4.52	97.3	8.3	1.77	102.1	13.2	3.15
Negative	80.8	-8.0	-2.00	77.1	-11.8	-2.50	79.0	-9.9	-2.25
<u>Trial 4</u>									
Positive	103.8	14.8	3.82	106.8	17.8	2.57	105.3	16.3	3.20
Negative	76.0	-12.9	-3.33	74.8	-14.1	-2.04	75.4	-13.5	-2.67
<u>Trial 5</u>									
Positive	104.1	15.3	3.09	113.7	24.5	4.57	108.9	19.9	3.83
Negative	71.7	-17.1	-3.44	75.6	-13.5	-2.51	73.7	-15.3	-2.98

was achieved for male than female broodstock in most mass selection lines.

Survival and Reproductive Success of Broodstock

Survival of family selection broodstock in 6-m tanks was extremely low, ranging from 3.3% to 30% (Table II). Within 6-m tanks, 9% to 71% of surviving females were classified as reproductively active, based on the presence of advanced cement gland development or attached eggs. At the time of broodstock and offspring collection from 6-m tanks, densities of offspring ranged from 0 to 3.5 per m² (Table II). In each family selection line, reproduction occurred in 2 of the 3 replicate tanks (Table II). All females classified as reproductively active subsequently spawned within a 2-week period.

Survival of mass selection broodstock within 2.4-m pools ranged from 25% to 100% (Table III). No reproduction occurred in pools prior to collection of mass selection broodstock, at which time 60% to 100% of surviving females within pools were classified as reproductively active (Table III). Many mass selection females classified as reproductively active failed to spawn in holding tanks, in spite of maintaining cement gland development for 180 days after removal from the 2.4-m pools.

Growth and Survival of Offspring

Growth in total length of offspring stocked as juveniles in the positive family selection trial averaged 2.8 mm per week (Table IV). Offspring stocked as third instar larvae had average growth rates of

Table II. Survival and reproductive success of negative, control and positive family selection Procambarus clarkii broodstock stocked into 6.0-m outdoor fiberglass tanks

Line	<u>Negative</u>			<u>Control</u>			<u>Positive</u>		
Tank	1	2	3	1	2	3	1	2	3
<u>Number Stocked</u>									
Males	5	5	5	13	13	13	5	5	5
Females	5	5	5	12	13	13	5	5	5
<u>Number Harvested</u>									
Males	1	0	2	2	3	1	3	2	4
Females									
Reproductive	4	0	1	4	1	0	0	1	0
Non-Reproductive	0	1	1	0	3	0	3	4	2
Total	4	1	2	4	4	0	3	5	2
Juveniles	0	4	17	37	45	0	97	41	0

Table III. Survival and reproductive success of negative (N), control (C) and positive (P) replicated mass selection Procambarus clarkii broodstock stocked into 2.4-m outdoor fiberglass pools

Replicate	<u>1</u>			<u>2</u>			<u>3</u>			<u>4</u>			<u>5</u>		
Line	<u>N</u>	<u>C</u>	<u>P</u>	<u>N</u>	<u>C</u>	<u>P</u>	<u>N</u>	<u>C</u>	<u>P</u>	<u>N</u>	<u>C</u>	<u>P</u>	<u>N</u>	<u>C</u>	<u>P</u>
<u>Number Stocked</u>															
Males	5	5	5	6	6	6	6	6	6	6	6	6	4	4	4
Females	5	5	5	6	6	6	6	6	6	6	6	6	4	4	4
<u>Number Recovered</u>															
Males	5	5	5	5	5	2	6	3	2	5	5	5	4	2	3
Females															
Reprod.	2	5	5	4	4	1	3	2	4	3	3	4	3	3	2
Non-Reprod.	1	0	0	0	0	0	0	0	0	1	2	0	1	1	0
Total	3	5	5	4	4	1	3	2	4	4	5	4	4	4	2
<u>Number of Spawns</u>															
	1	2	0	1	1	0	3	2	2	3	2	3	3	2	2

Table IV. Stocking dates, harvest dates and average growth rates of Procambarus clarkii offspring in family and replicated mass selection trials

<u>Trial</u>	<u>Stocking date</u>	<u>Harvest date</u>	<u>Days Growth</u>	<u>Growth (mm/week)</u>
<u>Positive</u>				
<u>Family</u>				
<u>Selection</u>	10/17/86 ^a	12/07/86	50	3.0
<u>Negative</u>				
<u>Family</u>				
<u>Selection</u>	11/19/86	05/08/87	170	3.5
<u>Mass</u>				
<u>Selection</u>				
Trial 3	01/02/87	05/12/87	130	4.8
Trial 4	12/03/86	05/12/87	160	4.0
Trial 5	01/29/87	05/14/87	105	6.1

a: Stocked as juveniles.

3.5 mm per week in the negative family selection trial, and 4.8, 4.0, and 6.1 mm per week in the third, fourth, and fifth replicates of mass selection, respectively.

Survival of offspring stocked as juveniles in the positive family selection trial ranged from 77% to 97% (Table V). Average length of these juveniles at stocking ranged from 56.2 to 59.5 mm among pools, with no significant ($P > 0.05$) differences between lines or pools. Survival of offspring stocked as third instar larvae in the negative family selection study ranged from 70% to 90% (Table V). Survival of offspring stocked as third instar larvae in mass selection replicates ranged from 0% to 100% (Table V).

Response to selection

Density at harvest effected length at harvest ($P < 0.05$) only in the fourth mass selection replicate (Table VI). Effect of density on weight at harvest was also significant ($P < 0.05$) in the fourth mass selection replicate and in the negative family selection trial (Table VI). Length and weight data in other replicates were not adjusted for density.

No significant differences ($P > 0.05$) in total length or weight at harvest were observed between offspring of select and control lines in any trial (Table VI). Selected lines differed significantly ($P < 0.05$) in dressout percentage only in the fifth replicate of mass selection, which lacked control line offspring (Table VI). Rankings of selected lines varied independently for separate variables within and among selection trials. No trends in either response to selection

Table V. Survival (%) of Procambarus clarkii offspring in family and replicated mass selection trials

<u>Line</u>	<u>Positive</u>			<u>Control</u>			<u>Negative</u>		
<u>Replicate Pool</u>	1	2	3	1	2	3	1	2	3
<u>Positive</u> <u>Family</u> <u>Selection</u>	87	77	---	97	77	---	---	---	---
<u>Negative</u> <u>Family</u> <u>Selection</u>	---	---	---	87	70	77	90	90	87
<u>Mass</u> <u>Selection</u>									
Trial 3	93	93	93	57	57	73	87	100	100
Trial 4	27	20	10	0	93	10	67	37	90
Trial 5	87	80	93	--	--	--	80	83	83

Table VI. Mean total length (mm), total weight (g), and dressout percentage at harvest of Procambarus clarkii offspring in positive (P), negative (N) and control (C) lines in family and replicated mass selection trials

Trial	<u>Total Length</u>			<u>Total Weight</u>			<u>Dressout Percentage</u> ^a		
	P	C	N	P	C	N	P	C	N
<u>Positive</u>									
<u>Family</u>									
<u>Selection</u>	77.5	78.0	----	15.3	14.5	----	----	----	----
<u>Negative</u>									
<u>Family</u>									
<u>Selection</u>	----	91.5	92.7	----	30.4 ^b	32.2 ^b	----	20.2	19.4
<u>Mass</u>									
<u>Selection</u>									
Trial 3	95.2	95.6	98.2	24.3	26.2	27.6	21.1	21.9	19.8
Trial 4	102.4 ^b	98.5 ^b	97.4 ^b	34.3 ^b	32.4 ^b	26.8 ^b	22.8	14.8	20.5
Trial 5	98.2	----	99.0	26.7	----	25.8	18.2 [*]	----	24.4 [*]

a: Adjusted for significant ($P < 0.01$) total length effect in all cases

b: Adjusted for significant ($P < 0.05$) density effect

*: Significantly different ($P < 0.05$).

for growth or correlated responses of processing traits were apparent.

DISCUSSION

In spite of low survival and reproductive success of broodstock, brood sizes were normal (200-500 individuals per brood), and sufficient numbers of offspring were produced in all trials to replace parental populations. Many females in mass selection replicates maintained advanced cement gland development, normally indicative of mature ovaries, for prolonged periods (180 days) in holding tanks. Reasons for their failure to spawn were not clear, especially since other females in holding tanks spawned successfully.

Growth of offspring in 2.4-m pools was slow during winter months due to cooler temperatures (Penn 1943, Lutz 1983), as evidenced by comparing stocking dates and average growth rates of offspring stocked as third instar larvae in negative family selection and mass selection trials. Reasons for variation in within-pool survival are not obvious; variation has been reported previously in pool studies with P. clarkii (Craig 1985, Lutz and Wolters 1988). Low survival (e.g., 0% to 10%) is probably not the result of cannibalism, considering high survival rates reported in other pool studies with P. clarkii stocked as third-instar larvae (Craig 1985, Lutz and Wolters 1988) or juveniles (Lutz and Wolters 1986). Lutz and Wolters (1986) reported high survival rates of P. clarkii stocked as juveniles at densities of 1 to 16 per m².

Results of selection experiments often demonstrate discrepancies between heritability estimates derived from sib analysis and realized

heritabilities derived from selection responses. Falconer (1981) stated that prediction of response to selection based on heritability estimates from sib analysis is valid in theory for only one generation of selection, and reviewed causes of both asymmetrical responses to selection and discrepancies between sib-analysis and realized heritability estimates. Lack of response to selection for growth in these trials does not contradict previous findings from sib analysis. Traditional ANOVA-based and mixed model sib analysis of broodstock which produced the offspring in this study yielded heritability estimates not significantly different from 0.00 for growth traits in P. clarkii (Lutz and Wolters 1987, 1988).

Family selection, mass selection, or some other form of selection may provide the greatest amount of genetic gain in a particular trait from one generation to the next, depending on the heritability of the trait, the ability to measure the trait on animals to be saved as broodstock, and the reproductive biology of the organism in question. Advantages and appropriateness of various forms of selection to achieve genetic gains have been reviewed by Falconer (1981). Although family selection would be expected to yield a greater selection response than mass selection for traits with low heritabilities (Falconer 1981), this was not observed in the results of these studies. Such responses would be expected if growth traits exhibited no additive genetic variation in P. clarkii. This conclusion is also supported by previously reported heritability estimates for growth traits derived from sib analysis of P. clarkii (Lutz and Wolters 1987, 1988).

Utilizing a mixed model sib analysis, Lutz and Wolters (1987b) reported significant ($P < 0.01$) genetic correlations for growth in total length with abdomen meat weight and dressout percentage in P. clarkii, although genetic correlations for total weight with processing traits were not significant ($P > 0.05$). It is possible that only a slight amount of additive genetic variation exists in P. clarkii for growth traits but they are positively correlated with processing traits over this range of genetic variation.

Crawfish which produced the full-sib families from which broodstock in this study were selected were collected from ponds and ditches at one geographic location (Lutz and Wolters 1987a). It is unlikely that little additive genetic variation existed in this population specifically as the result of reduced gene flow, inbreeding, or drift. Large numbers of wild P. clarkii from several locations had been introduced into some collection ponds 2 years prior to the initial acquisition of broodstock, while other collection ponds had supported P. clarkii populations for as many as 12 years (Romaine 1976). Frequent high water levels facilitated immigration and emigration through ditches to and from other temporary and permanent habitats populated with P. clarkii.

In population dynamics studies of P. clarkii, Lutz (1983) noted that contemporaneous recruitment classes of approximately equal average total length grew at the same rate in two adjacent commercial crawfish ponds in spite of different densities and forage availability. Growth rates within P. clarkii recruitment classes varied so little that separate classes were recognizable through

harvestable size (Lutz 1983).

Falconer (1981) has suggested that traits most closely associated with fitness generally have low heritabilities, while traits which have little or no effect on fitness exhibit relatively high heritabilities. In the case of P. clarkii, it is probable that growth rate is closely linked to fitness in terms of survival and reproductive success. Natural populations of P. clarkii generally inhabit temporary or highly variable habitats such as sloughs, ditches, or swamps, which are greatly affected by variation in rainfall. Considering the importance of size for this species in terms of burrowing capacity and other aspects of survival, it is likely that P. clarkii was subjected to rigorous natural selection to maximize growth rate over the course of speciation. This conclusion is supported when comparing the growth rate of this species with those of related species occupying more stable habitats.

Little additive genetic variation for growth in P. clarkii may be supported by the findings of systematic and taxonomic studies of this and related species. Utilizing electrophoretic techniques, several studies have shown that various Cambarid and Astacid crawfish, and decapods in general, have very low average heterozygosity values, and in this respect, little genetic variation relative to the number of loci segregating (Nemeth and Tracey 1979, Brown 1981, Hedgecock et al. 1982, Attard and Pasteur 1984). Hedgecock and Nelson (1978) reported moderate levels of additive and dominance genetic variation in a laboratory population of lobsters (Homarus americanus) in spite of low heterozygosity levels reported for this species (Tracey et al. 1975).

CONCLUSIONS

Little additive variation exists for growth traits in P. clarkii as measured in this and previous studies. Results suggest that current harvesting practices in commercial ponds pose little threat of negative selection for growth on harvested populations. Genetic improvement of P. clarkii should not be discounted, however. Possible utilization of dominance effects in growth traits through crossbreeding and heterosis should be investigated as a practical method of genetic improvement of growth and processing traits. Methods of control over timing of P. clarkii reproduction must be improved prior to initiation of large scale selection or crossbreeding programs.

SUMMARY

Summary of Methods

Thirty-nine full-sib families of red swamp crawfish, Procambarus clarkii, nested within 15 half-sib families, were produced by randomly mating males to 2 or more females each. Thirty, third-instar offspring from each full-sib family were stocked at $6/m^2$ in separate 2.4 m diameter fiberglass pools planted with rice (Oryza sativa) for forage. Offspring were harvested from pools after 150 days and measured for growth, body size and processing traits. Growth traits were adjusted for the effect of density within pools; other traits were adjusted for total length.

Heritability estimates for all traits were calculated using ANOVA-based quadratics (Becker 1981) for all animals combined and for reproductively mature (Form I) males, immature (Form II and juvenile) males, and females separately. A second analysis was performed using a mixed model, yielding BLUE's (Best Linear Unbiased Estimators) of the fixed effects of sex and male maturity, Henderson's Method III variance and covariance components, and genetic and environmental correlations. Heritability estimates based on Method III components were calculated for comparison with previous ANOVA-based estimates. Estimates of genetic correlations were utilized to formulate selection indices to maximize gains in net economic worth, growth, and processing traits.

Offspring from each full-sib family were selected as broodstock

for family selection and 5 replicates of mass selection. Broodstock were maintained in outdoor tanks and pools prior to spawning and allowed to mate at random within lines. Offspring were stocked at $6/m^2$ in 2.4 m pools planted with rice for forage, and harvested after 50-170 days growth. Differences between lines in growth traits and dressout percentage were analyzed within replicates of family and mass selection.

Summary of Results

Estimation of sire, dam and sire + dam heritabilities from ANOVA-based variance components for all animals combined yielded no sire heritability estimates significantly different from 0.00 ($P > 0.05$). When sexes and states of males maturity were analyzed separately, only 2 sire heritability estimates significantly different from 0.00 ($P > 0.05$) were calculated: carapace length and dressout percentage in reproductively immature males. Both of these estimates appeared biased.

Mixed model analysis estimates of variance and covariance components for all animals combined, utilizing sex and state of male maturity as fixed effects, produced heritability estimates in close agreement with those from ANOVA-based variance components. However, mixed model analysis produced a higher, significant ($P < 0.05$) sire heritability estimate for dressout percentage. Although genetic correlations derived from variance and covariance components indicated a positive genetic correlation between growth in length and processing traits, sib analyses based on a traditional or mixed models yielded

sire heritability estimates for growth traits which were not significantly different from 0.00 ($P < 0.05$).

No significant response to selection for growth in length was observed. Additionally, no trend in correlated response for dressout percentage was observed among offspring in the various selection trials.

Summary of Conclusions

Results of these studies suggest that little additive genetic control over growth traits could be utilized in large-scale P. clarkii selection programs. This conclusion is supported by previously reported average heterozygosity levels for this and other crawfish species. Body size traits exhibit slight to moderate amounts of additive variation in P. clarkii. It may be possible to improve dressout percentage if body size traits are utilized collectively in a selection index, as indicated by the heritability estimate of this trait based on mixed model analysis.

Further Research Needs

Moderate levels of genetic improvement in processing traits would result in substantial increases in the value of cultured stocks of P. clarkii. Construction of more accurate indices to improve processing traits and response to selection based on these indices deserves further effort.

The role of dominance effects and their potential for utilization in genetic improvement of P. clarkii cannot be clearly evaluated from

the sib analysis and selection studies which comprised this research. Use of a diallel mating system utilizing geographically distinct populations of P. clarkii and subsequent evaluation of growth, body size and processing traits would be expected to provide additional information on additive variation in the species as a whole, and on the role of dominance genetic effects in expression of these traits.

Techniques for maintaining and spawning P. clarkii broodstock under artificial conditions (such as pools and indoor tanks) must be improved prior to the pursuit of large-scale selection or crossbreeding programs. One important aspect of such research should be control of timing and success of reproduction.

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VITA

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DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: Charles Gregory Lutz

Major Field: Wildlife & Fisheries Science

Title of Dissertation: Estimation of Heritabilities, Genetic Correlations, and Response to Selection for Growth, Body Size, and Processing Traits in Red Swamp Crawfish, Procambarus clarkii (Girard).

Approved:

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